Influence of Environmental Conditions on Flight Activity of *Plecotus townsendii virginianus* (Chiroptera: Vespertilionidae)

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ABSTRACT—Flight activity of the Virginia big-eared bat (*Plecotus townsendii virginianus*) was measured in relation to eight environmental variables during 1990 and 1991 in Lee County, Kentucky. Activity, measured as the mean nightly detection frequency of bats fitted with transmitters, was positively related to percent relative humidity and negatively related to moon phase and wind speed. Multiple regression analysis showed relative humidity to have the strongest association with flight activity of all the environmental variables tested. An explanation for this pattern was that bats reduced their foraging activity on nights of low relative humidity to avoid excess water loss because of extremes in vapor pressure deficits during flight. Other explanations for the observed activity patterns may exist, but they were not investigated in our study.

A wide range of abiotic environmental variables affect flight activity of bats, including sunlight, moonlight, temperature, wind speed, and precipitation. Sunlight inhibits flight activity and serves to synchronize circadian periodicity (Erkert et al. 1980). Moonlight reduces flight activity (Erkert 1974) and is known to induce shifts in foraging patterns (Fenton et al. 1977). Flight activity of bats increases with temperature, with shorter activity periods on cooler nights (Anthony et al. 1981) and extended bouts of activity on warmer nights (O'Farrell et al. 1967). Sufficiently strong winds suppress flight activity (O'Farrell et al. 1967), but the influence of slower air speeds, if any, is unknown.

Responses of bats to precipitation is not consistent among, or even within, species. Heavy rainfall reduced flight activity of *Pipistrellus pipistrellus* (Stebbings 1968), but did not do so in another study (Swift 1980). The timing of rainfall events is important (Felton et al. 1977), with rain at dusk known to delay nightly emergence in *Nycticeius humeralis* (Watkins 1972).

In contrast, effects of relative humidity on flight activity of bats have been suggested (Watkins 1972, Lacki 1984) but quantitative data are lacking. Studies have demonstrated the importance of water balance to bats under both laboratory (Bassett 1980, Bassett and

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Wiebers 1980) and free-ranging conditions (Kurta et al. 1989, Kurta et al. 1990). This would suggest that selection for adaptations to minimize water loss should evolve in bats, particularly in association with flight because of the high surface area to volume ratio of bat wings.

Bats inhabiting arid environments show a direct relationship between urine concentrating ability and evapotranspiration to precipitation ratio (Bassett 1986). In wetter regions, bats should encounter fewer problems of water balance. Flexibility in foraging strategy, such as reduced activity on less humid nights (i.e., increased vapor pressure deficits), should help to maintain water balance.

Using radio telemetry we monitored flight activity of a temperate zone insectivorous bat, *Plecotus townsendii virginianus*, and related observed activity patterns with data for local environmental conditions. We tested the hypothesis that flight activity of *P. t. virginianus* is reduced as relative humidity declines, which would be expected if water balance is a critical selective pressure for temperate zone bats.

METHODS

The study area was located in the Cumberland Plateau, Lee County, Kentucky. Lee County is 80% forested and sparsely populated by humans (Newton et al. 1974). Mixed mesophytic forest is the dominant habitat (Braun 1950) with most stands being second growth timber because of past logging practices. The climate of the region is temperate, characterized by warm and humid summers and moderately cold winters. Average maximum and minimum temperatures are 34C in August and -18C in January (Newton et al. 1974). Average monthly precipitation is 9 cm (Newton et al. 1974). July and October are the wettest and driest months, respectively. Additional site details are provided by Adam et al. (1994).

Sixty bats were fitted with transmitters during 1990 and 1991, 30 each summer. Because this subspecies is very sensitive to disturbance (Bagley 1984), we studied males in 1990 and females in 1991 and addressed any problems that occurred with males in 1990 before handling females in 1991. Bats were mist-netted as they emerged from bachelor and maternity roosts, along cliffs, and on an abandoned logging road. Bats were weighed, sexed, aged, and then fixed with a 0.8-g transmitter (Type BD-2A, 172-173 MHz; Holohil Systems, Ltd., Ontario, Canada, and Wildlife Materials, Inc., Carbondale, Illinois) on the dorsum between the scapulae. The surface was prepared by trimming the fur with scissors and applying surgical cement designed to hold the transmitter for about 10 days.

Three telemetry periods, each spanning five nights, were conducted in each year. In 1990 male bats were radiotracked from 2 to 6 June (n = 9 bats), 16 to 20 July (n = 10), and 6 to 10 August (n = 11). In 1991 females were tracked from 10 to 14 May (n = 9), 17 to 21 June (n = 10), and 5 to 9 August (n = 11). Bats were tracked from both fixed and mobile stations. Fixed stations were positioned on the top of cliffs enclosing a hollow with either a bachelor or maternity roost. Distances between fixed stations averaged 857 m in 1990 and 509 m in 1991. Mobile stations were along road routes throughout the surrounding areas. Three TRX1000s receivers (Wildlife Materials, Inc., Carbondale, Illinois) were used to locate bats, with an additional TRX2000s receiver used in 1991. Receivers were coupled to a 3- or 5-element yagi antenna. Signals were searched for at 20-minute intervals from sunset to sunrise. Bats may have been detected in multiple intervals by more than one receiver.

Telemetry data were organized into nightly rates of bat activity by converting signal responses into mean nightly detection frequencies (*NDF*) calculated as

$$NDF = \sum_{j=1}^{t} \left(\sum_{i=1}^{n} (d/o)/n \right) t^{-1}$$

where *NDF* = mean nightly detection frequency, t = number of time intervals post-sunset, n = number of bats with transmitters, d = number of receivers detecting a bat in an interval, and o = number of receivers operating in an interval.

Patterns of activity were also derived for each sampling period by converting signal responses to mean detection frequencies per time interval (*TIDF*) calculated as

$$TIDF = \sum_{j=1}^{k} \left(\sum_{i=1}^{n} (d/o)/n \right) k^{-1}$$

where *TIDF* = mean detection frequency per time interval, and k = number of days sampled.

Nightly environmental conditions were obtained from the Heidelberg, Kentucky, weather station located 11 km, from the bachelor roost. The foraging radius of bats from the bachelor and maternity colonies was large (Adam et al. 1994), rendering sampling for environmental conditions throughout the study site impractical. Data for eight variables were analyzed: daily maximum temperatures (°C), daily minimum temperature (°C), total precipitation the day of sampling (cm), total precipitation on the day preceding sampling (cm), average daily relative humidity (%), average daily wind speed (km/hr), average daily barometric pressure (millibars), and moon phase (% of full moon illumination).

We initially tested *NDF* against all environmental variables separately using simple linear regression, and only those variables meeting the 0.10 probability level were retained. Backwards stepwise multiple regression was then used for modeling *NDF* against environmental variables. A probability of >0.10 was used for removal of a variable from the model. Data for 1990 and 1991 were combined for analysis. Differences between years (sexes) were checked using analysis of variance (ANOVA), with the day of sampling as a block effect. Relative humidity and moon phase were arcsine transformed to correct for nonnormality of the data.

RESULTS

All bats that were fitted with transmitters were adults except for five juvenile males in August 1990 and one juvenile female in August 1991. Data for body mass and reproductive condition are presented elsewhere (Adam et al. 1994). Transmitters did not appear to adversely affect the bats. Bats showed no difficulty flying upon release and were located at considerable distances from known roosts. During August 1991, two females were captured which had previously been fitted with a transmitter. Masses for these females were not different from the average mass of other females captured during that period. Although transmitters on some bats emitted signals for up to 10 days, we considered 5 days to be the normal life of transmitters in this study. Data from all 60 bats were used, regardless of the life of the transmitters.

Analysis of variance demonstrated no day effect ($F = 2.81$; df = 4, 20; $P > 0.10$) and no interaction between day and year ($F = 1.48$; df = 4, 20; $P > 0.10$). Activity rates were higher in 1991 than in 1990 ($F = 22.9$; df =1, 20; $P < 0.0001$) (Fig. 1). It is unclear whether this difference was due to sex or varying conditions between summers, as males and females were not tested in both summers.

Bats did not emerge to forage until 30 to 45 minutes post-sunset (Fig. 1). Males in 1990 exhibited a pattern with highest activity during the first few hours of the night (Fig. 1a). The activity of females in 1991 was more sustained throughout the night (Fig. 1b). Females in these periods were either pregnant (May) or lactating (June) (Adam et al. 1994), suggesting the use of night roosts and/or shorter foraging bouts which allowed them to return to the maternity roost to nurse their young.

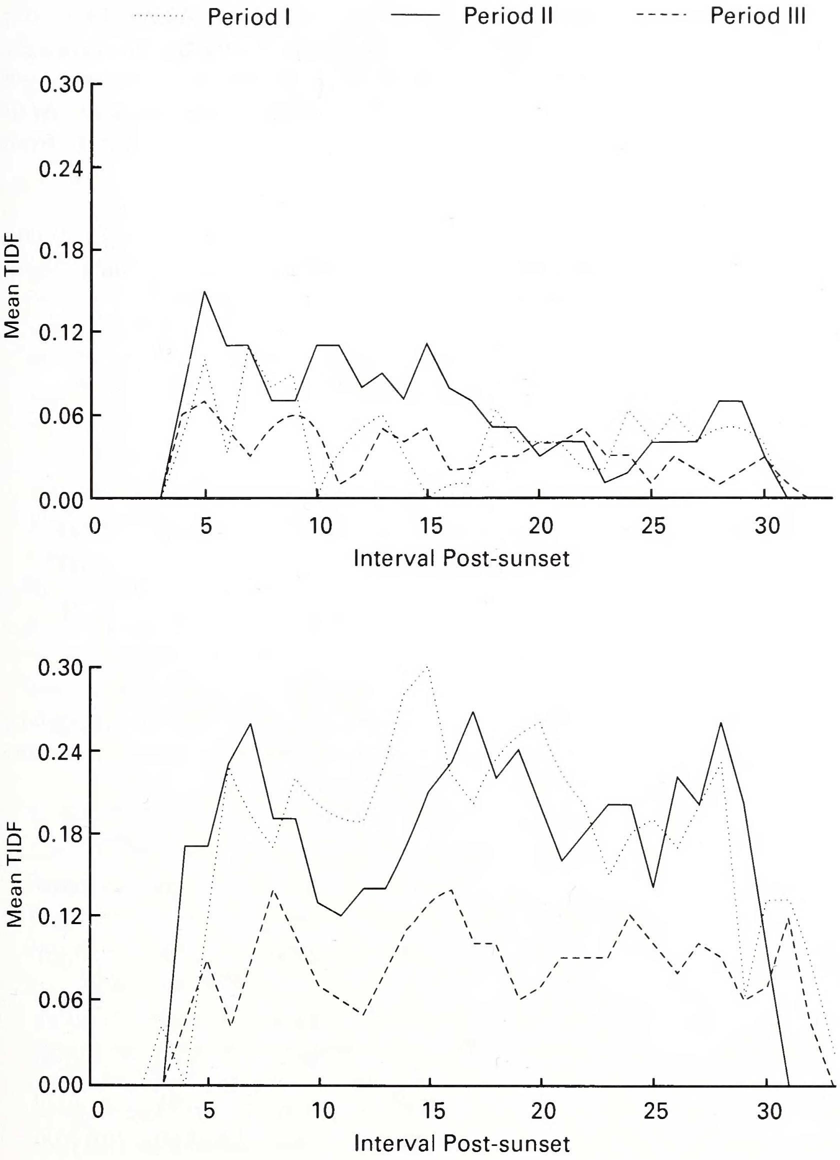

Fig. 1. Mean frequency of detection by 20-minute time intervals (*TIDF*) post-sunset for *P. t. virginianus* comparing sampling periods; males (a): Period I = June, Period II = July, Period III = August 1990; females (b): Period I = May, Period II = June, Period III = August 1991), Lee County, Kentucky.

Three environmental variables were related to *NDF* (Table 1); *NDF* was positively associated with percent relative humidity, and negatively related to both wind speed and moon phase. Stepwise regression demonstrated a significant ($F = 5.93$, $P = 0.0073$, $R^2 = 0.30$) relationship of *NDF* with relative humidity and moon phase, eliminating wind speed from

Table 1. Regression analyses of mean nightly detection frequency (*NDF*) with environmental variables for *P. t. virginianus*, Lee County, Kentucky, summers 1990 and 1991.

Regression	Environmental variable	Coefficient	SE	*P*
Simple	Relative humidity	0.23	0.085	0.01
	Moon phase	-0.06	0.026	0.03
	Wind speed	-0.01	0.004	0.04
Multiple	Relative humidity	0.20	0.083	0.02
	Moon phase	-0.05	0.025	0.06

Table 2. Values for nightly detection frequency (*NDF*) and environmental variables for *P. t. virginianus*, Lee County, Kentucky, summers 1990 and 1991.

Variable	Mean	CV	Range High	Range Low
NDF	0.08	88.5	0.30	0.01
Relative humidity (%)	0.77	11.0	0.97	0.64
Moon phase (%)	0.44	85.2	0.99	0.00
Wind speed (km/hr)	10.80	32.0	20.50	6.40
Barometric pressure (mb)	1,017.00	0.4	1,024.00	1,011.00
Maximum temperature (C)	28.40	12.3	33.30	18.90
Minimum temperature (C)	16.00	19.8	21.10	11.10
Precipitation (cm)	0.61	221.0	5.84	0.00
Prior precipitation[1] (cm)	0.67	204.0	5.84	0.00

[1] Represents rainfall during the day prior to sampling.

the final model. No pattern was observed between significant and nonsignificant environmental variables using coefficients of variation (Table 2), indicating no bias because of differences in the amount of variability in these sets of variables.

DISCUSSION

We found a direct relationship between flight activity of *P. t. virginianus* and ambient relative humidity, with bats exhibiting reduced activity on nights with lower percent relative humidity. Using mist-net captures as a measure of activity, Lacki (1984) observed a similar pattern for *Myotis lucifugus* and suggested reduction in flight activity as a behavioral mechanism for avoiding water loss on nights when ambient conditions created large vapor pressure deficits.

Bats experience water loss in flight and can lose water because of roost conditions (Carpenter 1969). Substantial water loss accompanies digestion in *M. lucifugus* (Bassett and Wiebers 1980) with water balance in female *M. lucifugus* (Kurta et al. 1989) and female *Eptesicus fuscus* (Kurta et al. 1990) influenced by reproductive condition. Because water loss by bats is dependent on ambient temperature and water vapor pressure under laboratory conditions (Bassett 1980) and water loss increases with higher levels of flight activity (Studier 1970), we suggest that our data support the existence of a behavioral response by bats for avoiding extremes in vapor pressure deficits during flight.

Factors such as prey activity and availability may also contribute to the observed activity patterns, but were not investigated in our study. Data comparing the abundance of insect prey with ambient relative humidity are sparse; however, in one study no association was found between relative humidity and activity of moths (Mizutani 1984). Moths are the predominant item in the diet of *P. t. virginianus* (Sample and Whitmore 1993).

The inverse relationships we observed between activity of *P. t. virginianus* and both moon phase and wind speed are consistent with other findings reported in the literature (O'Farrell et al. 1967, Erkert 1974, Fenton et al. 1977). Whether avoidance of moonlight by *P. t. virginianus* was because of predators or availability of insect prey or both is unclear. Several species of owls were common in the study area, and abundance of insect prey has been shown to be negatively related to moon phase (Anthony et al. 1981). Observations at a maternity colony of a related subspecies, the Ozark big-eared bat (*P. t. ingens*), found no patterns between flight activity and indicies of moon brightness (Clark 1991).

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